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New suoid remains (Mammalia, Artiodactyla) from the Late Miocene of Haritalyangar, India

Anek R. SANKHYAN[1] Olivier CHAVASSEAU[2,*]

(1 *Palaeo Research Society*, *IPH Colony* Ghumarwin, Himachal Pradesh- 174021, India)
(2 *Laboratoire Paléontologie Evolution Paléoécosystèmes Paléoprimatologie* (*PALEVOPRIM*) UMR-CNRS 7262, Université de Poitiers, 6 rue M. Brunet, 86073 Poitiers, France
*Corresponding author: olivier.chavasseau@univ-poitiers.fr)

Abstract We report here a number of mandibular, maxillary and dental fossil remains of Indian Suoidea from the Middle Siwalik of Haritalyangar area in Bilaspur District of Himachal Pradesh, North India. Haritalyangar is well known for the diversity of the Late Miocene fauna and the hominoids and other primates. The suoid remains were collected by one of the authors (ARS) during different field seasons and their localities were plotted on the map, along with those of the proboscidean reported recently, including the hominoid localities. The fossil localities are spread over the 'Lower Alternations' and the 'Upper Alternations' from Makkan Khad to Sir Khad. We have assigned the fossils into three genera, *Propotamochoerus* (*P. hysudricus*), *Hippopotamodon* (*H. sivalense*) and *Yunnanochoerus* (*Y. dangari*). *Propotamochoerus hysudricus* represents the most common suid in the Middle Siwaliks. The new remains of the suoid *Yunnanochoerus dangari* further documents this rare palaeochoerid only known in the Haritalyangar area by a few fossils. The new suoid remains show clear affinities with the Nagri fauna of the Pakistan Siwaliks. Biochronological correlations with the Potwar Plateau based on suoids indicate an age bracket of ~10–9 Ma for the 'Lower Alternations' of Haritalyangar, close to the bracket mostly recently proposed on the basis of magnetic polarity stratigraphy.

Key words Middle Siwalik, Late Miocene, Suoidea, *Yunnanochoerus*, *Propotamochoerus*, *Hippopotamodon*

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1 Introduction

The suoids represent a major group of medium-sized artiodactyls in the mammalian communities of the Neogene period of the Siwalik Hills. Many authors have revealed a rich paleodiversity of Siwalik suoids dominated by suids (Falconer and Cautley, 1847; Falconer, 1868; Lydekker, 1884; Pilgrim, 1926; Lewis, 1934; Colbert, 1935; Prasad, 1970; Nanda, 1982;

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Vasishat, 1985; Pickford, 1988; Made, 1997, 1999; Khan et al., 2013; Batool et al., 2015; Dar et al., 2019). During the Early and Middle Miocene, the Siwalik suoids are mostly represented by suids such as the listriodontine *Listriodon* and the tetraconodontine *Conohyus*. Suoids are rare and only documented by the poorly known genus *Pecarichoerus*. During the early Late Miocene, *Listriodon* and *Conohyus* disappeared and the suines *Propotamochoerus hysudricus* and *Hippopotamodon sivalense* became the dominant suoids with an abundant fossil record and a widespread distribution across the Indian subcontinent. Other suoids are comparatively much less abundant and are represented for instance by the large tetraconodontine suid *Tetraconodon magnus* and small tetraconodontine *Lophochoerus*. The palaeochoerid *Yunnanochoerus* is also a rare taxon present in the Late Miocene of the Siwaliks. The Siwalik suoids are less diverse in the Pliocene and Pleistocene and are represented by the genera *Sivachoerus*, *Hippohyus*, *Sivahyus* and *Sus*. The Siwalik suoids provide precious information on the evolution of Asian Neogene suoids in Southern Asia. The Siwalik suoids are also interesting in the perspective of further understanding the evolution of the Old Word suoids since they possess affinities with faunas from Europe, Africa and other regions of Asia such as Western Asia, China or Southeast Asia.

The fluvial sediments of the Siwalik Group are exposed along the southern Himalayan foothills covering a great distance of about 2400 km between the river Indus in the west and the river Irrawaddy in the east comprising of over seven-kilometer-thick Himalayan wash out molasses, spanning a great period of over 15 million years from Early Miocene to Middle Pleistocene (Pillans et al., 2005). The thickness of these deposits varies from 950–1200 m (Barry et al., 2002). The Potwar segment of the Middle Siwalik is the widest and has yielded the richest assemblage of mammalian and hominoid fossil remains (Pilbeam et al., 1977a, b, 1980; Barry et al., 2002). These sediments are comprised of alternating sequences of sandstone, claystone/siltstone and rarer conglomerates (Pilbeam et al., 1977a; Barry et al., 2002). Magnetic polarity and stratigraphic dating suggest about 11 to 3.5 Ma to the Middle Siwalik sedimentation (Johnson et al., 1982; Tauxe and Opdyke, 1982; Brozovic and Burbank, 2000; Barry et al., 2002). Next to Potwar, the Upper Miocene strata of Haritalyangar are noted for the presence of the hominoids *Sivapithecus* and *Indopithecus* (Sankhyan, 1985; Pillans et al., 2005). A pliopithecid primate, *Krishnapithecus*, is known from Haritalyangar (Chopra and Kaul, 1979; Sankhyan et al., 2017), which also recently yielded a rare Chameleon from the *Krishnapithecus* site (Sankhyan and Čerňanský, 2016) and proboscidean remains (Sankhyan and Chavasseau, 2018). Compared to Potwar Siwalik, the suid remains, have sparingly been reported from Haritalyangar (Vasishat, 1985). This study, therefore, makes a significant contribution to the Late Miocene Suoidea by reporting rare mandibles and maxillae of suid fossils, collected by one of us (ARS), who also mapped the localities (Fig. 1). The new suoid localities are at Karan, Kherin, Dholkhana, Bhapral and Barog in the "Upper Alternation" (correlated with the Dhok Pathan Formation of the Potwar Siwalik), exposed 3 to 5 km east of Haritalyangar. The "'Lower Alternations'" (correlated with the Nagri Formation of Potwar Siwalik) at Dangar, Hari and Targhel yielded suoid fossils. They represent two main genera,

Propotamochoerus and *Yunnanochoerus*. The presence of the genus *Hippopotamodon* is also documented by two specimens.

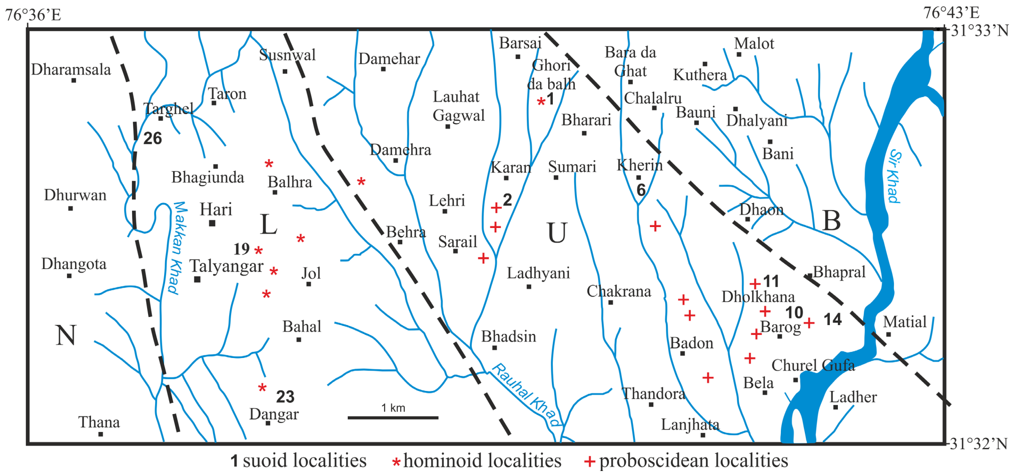

Fig. 1 Map of the region of Haritalyangar showing the localities that yielded fossil suoids
The hominoid and proboscidean bearing localities are also indicated. Suoid Localities: 1. Ghori S; 2. Kutla /Karan E; 6. Kherin W; 10. Dholkhana lower; 11. Dholkhana Upper; 14. Barog S / Cap-Ridge; 19. Hari mid Scarp; 23. Dangar East (Dhagiala); 26. Targhel SW. B= Boulder Conglomerate
Dashed lines: limits between the formations (modified after Johnson et al., 1983);
L. 'Lower Alternations' (=equivalent to the Nagri Fm. of the Siwaliks of Pakistan);
N. Nahan Formation (=equivalent to the Chinji Fm. of the Siwaliks of Pakistan);
U. 'Upper Alternations' (= equivalent to the Dhok Pathan Fm. of the Siwaliks of Pakistan)

2 Materials and methods

One of us (ARS) collected the fossils from localities falling between the Makkan Khad in the west and the Sir Khad in the east (Fig. 1). The specimens are housed and displayed in the Palaeo Museum at Ghumarwin, 15 km south of Haritalyangar. ARS properly cleaned, reconstructed some and prepared for photography and metric study in the Palaeo laboratory of the Palaeo Museum. He also did mapping of the sites and made stratigraphic observations. The measurements were taken a digital caliper with a precision of 0.01 mm and are given at 0.1 mm. The measurements are presented in Tables 1 and 2. Body mass estimates of the Haritalyangar suoids were calculated based on the equation for artiodactyls of Legendre (1989): ln (bodymass) = 1.528 × ln (m1 surface) +3.5503. Because the m1s are often worn, we also used body mass estimates of Damuth (1990) for ungulates based on m2 length ($\log_{10}$ (bodymass) = 3.07 × $\log_{10}$ (m2 length) +1.07). For maxillae, the Damuth (1990) regressions for M2 length ($\log_{10}$ (bodymass) = 3.03 × $\log_{10}$ (M2 length) +1.06) and M1 area ($\log_{10}$ (bodymass) = 1.50 × $\log_{10}$ (M1 area) +1.33) were used because they show the highest correlations among available variables.

Institutional abbreviations: GSI, Geological Survey of India (Calcutta). Comparative studies of the Haritalyangar material were made according to published data and direct

observations of the suoid material from the H-GSP collection; H-GSP, collections of the Harvard-Geological Survey of Pakistan expeditions housed in Harvard University; HTA, Haritalyangar fossil collection housed in the Ghumarwin Palaeo Museum (Himachal Pradesh, India). The adopted dental nomenclature is that of Orliac et al. (2015).

Table 1 Upper teeth measurements of the new suoid material from Haritalyangar, India (mm)

Specimen	Locality number	Taxon	length × breadth				
			P3	P4	M1	M2	M3
HTA-42a	6	*P. hysudricus*	13.2×12.2	12.0×14.6	14.9×15.1	–×19.6	28.9×20.2
HTA-42b	6	*P. hysudricus*	–	12.6×14.6	14.8×–	21.4×19.3	28.7×20.8
HTA-140a	23	*P. hysudricus*	–	–	–	21.2×19.2	29.5×20.4
HTA-140b	23	*P. hysudricus*	–	–	14.2×13.8	21.1×19.4	29.3×20.2
HTA-126a	19	*P. hysudricus*	–	13.1×14.4	14.8×14.6	–	–
HTA-5/79	6	*P. hysudricus*	–×9.1	11.0×12.4	–	–	–
HTA-20	1	*H. sivalense*					>35×>30

Table 2 Permanent lower teeth measurements of the new suoid material from Haritalyangar, India (mm)

Specimen	Locality number	Taxon	length × breadth					
			p2	p3	p4	m1	m2	m3
HTA-8a	1	*P. hysudricus*	9.8×4.0	13.9×5.8	14.6×9.5	14.6×11.6	18.8×14.3	30.0*×15.2*
HTA-8b	1	*P. hysudricus*	10.9×4.9	14.2×5.9	15.1×10.1	14.6×12.6	18.9×14.7	31.8×16.3
HTA-126b	19	*P. hysudricus*	–	–	–	19.4×14.6	24.1×18.2	–
HTA-141	23	*P. hysudricus*	–	–	–	17.9×12.5	22.9×16.4	–
HTA-154	23	*Y. dangari*					20.6×11.7	21.1×11.6

* estimated measurement.

3 Systematic paleontology

Suoidea Gray, 1821

Suidae Gray, 1821

Suinae Gray, 1821

***Propotamochoerus* Pilgrim, 1925**

***Propotamochoerus hysudricus* (Stehlin, 1899-1900)**

Holotype GSI B30, right hemi-mandible fragment with p3–m3.

Distribution and temporal range Late Miocene of South Asia (India, Pakistan) and Southeast Asia (Myanmar; Pickford, 1988; Sein et al., 2009; Jaeger et al., 2011; Chavasseau et al., 2013); 10.2–6.5 Ma in the Potwar Plateau (Siwaliks of Pakistan) (Barry et al., 2002).

New material HTA-8a and HTA-8b, right and left mandible with p2–m3 belonging to a single individual from Loc. No. 1, Ghori da Balh; HTA-42a and HTA-42b, left maxilla with P3–M3 (42a) and right maxilla with P3 roots and P4–M3 (42b) belonging to a single individual from Loc. No. 6, Kherin SW along the foot track to Badon. One central incisor was also associated with these maxillae; HTA-140a and 140b, right maxilla with M2–M3 (140a) and right maxilla with M1–M3 (140b); HTA-5/79, right maxilla with the distal part of P3 and P4; HTA-126a, right maxilla with P4–M1; HTA-126b, right mandibular fragment with m1–m2;

HTA-141, right mandibular fragment with m1–m2; HTA-50b, left m2 on a piece of mandibular corpus; HTA-7, left dp4 on a piece of mandibular corpus; HTA-65 right dp4.

Description of the new material Upper dentition: HTA-42a and HTA-42b preserve P3–M3 and P4–M3 (Fig. 2C, D). The P3 is a three-rooted tooth with a large mesial root and two smaller distobuccal and distolingual roots. The crown, visible on the left hemi-maxilla, is trapezoidal in shape. The tooth is composed of a large buccolingually compressed paracone, which displays a mesiodistally elongated wear pattern, and a protocone. The precrista is not visible due to wear but the distal part of the distocrista is observable. This crest is mesiolingual and connects to the distal cingulum, which reaches to the distobuccal part of the crown. No metacone is visible. The buccal wall is rather flat and perpendicular to the mesial and distal walls. The protocone is located distobuccal to the paracone and is much smaller than it. This cusp presents a mesiolingually oriented wear surface and is separated from the paracone by a rather mesiodistal valley.

The P4 has a square outline and is comprised of three cusps. The paracone and the metacone are equal-sized and widely spaced. A vertical depression on the buccal wall distinctly separates these two cusps. The protocone has a central position along the mesiodistal axis. Accessory conules are present in the central valley of the tooth, against the buccal cusps. A distal style, better expressed on the left P4, is present against the protocone. Thick mesial and distal cingula are present.

The molar row shows a clear gradient of wear from front to rear, the M1s being completely worn while the M3s are only moderately worn on the first lobe and lightly worn on the distal lobes. The size increase from M1 to M3 is moderate. The M1s are square and slightly larger than P4s. The buccal part of the right M1 is broken away. Due to heavy wear, the only crown feature retrievable is the presence of a laterally expanded accessory cusp at the lingual end of the median valley. The mesial part of the left M2 is missing. Most of the occlusal details of the M2s are worn away except the thick mesial cingulum, the laterally expanded lingual accessory cusp between the lobes of the crown, and a small central distocone. The M3s show a mesially-placed triangular paraconule fused with a thick mesial cingulum. A large triangular centroconule is present and connected to the lingual cusp present at the terminus of the median valley. The groove separating the centroconule from the metaconule is very shallow. A lingually-placed distocone that is as large as the main cusps forms the third lobe of the tooth together with a smaller cusp and two tiny ectostyles.

Mandibular remains: HTA-8a and HTA-8b (Fig. 2A, B) are left and right mandibular rami with full array of dentition form p2–m3 belonging to a single individual. They were collected from Ghori da balh, just above the gray shale layer that previously yielded a m2 belonging to a rare late survivor of *Sivapithecus* (Sankhyan, 1985). The p2 is double-rooted. It is a narrow and elongated tooth with a single cusp (protoconid) from which two crests depart. The protoconid is mesially positioned so that the postprotocrisitd is longer than the preprotocristid. A small mesial cingulid is present. The width of the tooth is constant from back to rear. The p3, also

double-rooted, is larger than the p2 and also a narrow and elongated tooth. Compared to the p2, the protoconid is slightly more bulbous and the distal lobe is wider than mesial one. The distal part of the p3 is broken so that it is not possible to know if a small hypoconid was present or not. The p4 is more molarized than the other premolars, is distinctly wider, and shows a rectangular outline. A large protoconid and a smaller metaconid placed distolingually to it are present on the first lobe. Mesiodistal pre- and postprotocristid connect the protoconid to the mesial cingulid and a large hypoconid being the only cusps of the talonid. The hypoconid is

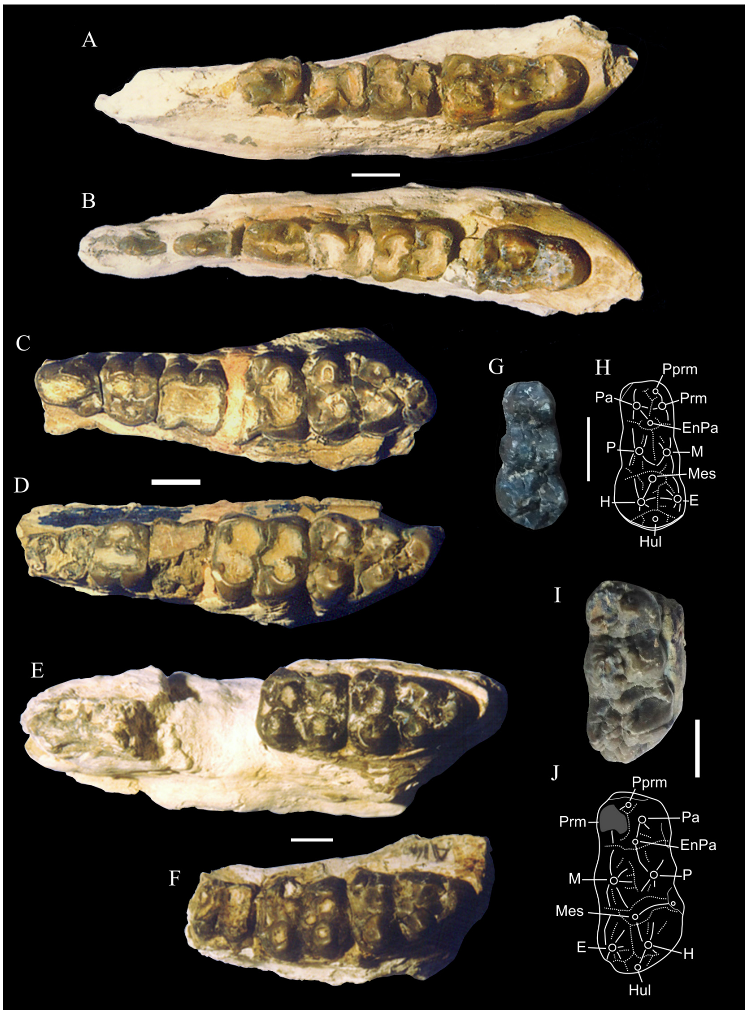

Fig. 2 New material of *Propotamochoerus hysudricus* and *Hippopotamodon sivalense* from Haritalyangar
A–H. *Propotamochoerus hysudricus*: A. HTA-8a, right mandible with p4–m3 (p2–p3 not displayed); B. HTA-8b, left mandible with p2–m3; C. HTA-42a, left maxilla with P3–M3; D. HTA-42b, right maxilla with P4–M3; E. HTA-140a, right maxilla with M2–M3; F. HTA-140b, right maxilla with M1–M3; G, H. left dp4, HTA-7 (G) and interpretive drawing (H); I, J: *Hippopotamodon sivalense* right dp4, HTA-63 (I) and interpretive drawing (J). All specimens are figured in occlusal view. Scale bars equal 1 cm
Abbreviations: E. entoconid; EnPa. endoparaconulid; H. hypoconid; Hul. hypoconulid; M. metaconid; Mes. mesoconulid; P. protoconid; Pa. paraconid; Pprm. preprimonid; Prm. primonid

high and reaches two thirds of the height of the protoconid. Deep buccolingual valleys separate the hypoconid from the trigonid cusps. There is no diastema in the premolar row.

The molars increase moderately in size from m1 to m2. The m1s are heavily worn and m2s are very worn. The trigonid of the right m3 is broken. The m3s are rectangular, the width of the tooth decreasing gently from the first to the third lobe. No lateral cingulid is visible. The valley between the two mesial lobes is interrupted by a mesoconulid and a endometaconulid, which are only separated by a shallow groove. This valley remains deep between the metaconid and the entoconid and is not closed laterally by stylids. The third lobe is elongated and bears a large and central hypoconulid as well as a large hexagonal prehypoconulid and smaller endo-and ectostylids. The ramus is broken just behind the M3s, suggesting the absence of a retromolar gap.

The lower jaws fragments with m1–m2 (HTA-126b and 141) are less worn and yield additional characters: a moderately thick cingulum is present mesially and partly around the protoconid. A small paraconid is located mesially against the protoconid and the metaconid. This cusp is slightly shifted lingually relative to the long axis of the tooth and is separated from the protoconid by a groove. The groove between the hypoconid and the entoconid is incomplete or much weaker. The hypoconulid is small on m1 but a much larger cusp on m2.

The dp4 HTA-7 (length: 19.9 mm; breadth: 9.3 mm) is a trilobate and elongated tooth (Fig. 2G, H). The trigonid is bilobate. The mesial lobe is composed of two close cusps, paraconid and primonid, separated by a deep groove. A small accessory cusp, the preprimonid, is located mesially. The second lobe is composed of two cusps, the protoconid and the metaconid connected distally by the junction of a postmetacristid and a postprotocristid. The trigonid basin is notched on both sides. The third lobe shows a wide talonid basin, two well-spaced hypoconid and entoconid, and a small central hypoconulid accompanied by a distal cingulid. The valley between the trigonid and the talonid is deep but closed lingually by a cingulid. A poorly individualized mesoconulid is present and connected to the hypoconid by a cristid obliqua. The talonid is distinctly wider than the trigonid. This widening is prominent on the lingual side of the tooth. The buccal side of the tooth is rather flat with only a small ectoflexid between the second and third lobes. A second dp4, HTA-65 (length: 22.0 mm; breadth: 9.5 mm), displays similar size and morphological characteristics expect for a more inflated preprimonid.

Discussion The new material fits well in terms of measurements and morphology to *Propotamochoerus hysudricus*, a common suid in the Late Miocene of Southern and Southeast Asia characterized by medium size, weakly to moderately deep furrows on molars, lower molars with poorly developed lateral cingulids and relatively simple talonids/expansion of talonids, simple and non-inflated lower premolars, P4 with small to medium sized accessory conules, and no diastema is the premolar and molar tooth row. The sample of Haritalyangar corresponds well to the range of size for this species sampled in the Potwar Siwalik with HTA-42a/b and HTA-8a/b representing small-sized individuals and HTA-126b a large individual close to the upper limit of this species. The two dp4 match in size those of *P. hysudricus* (Pickford,

1988). Although its first lobe is damaged, the dp4 of the *P. hysudricus* specimen H-GSP 5112 (Pickford, 1988:fig. 110) also shows an identical outline (distinct increase in breadth toward the third lobe) with specimen HTA-7 and HTA-65. The two dp4s from Haritalyangar are thus allocated to *P. hysudricus*.

The status of the species *P. hysudricus* has been subject to debate in the literature. *Propotamochoerus* is a widespread genus in the Late Miocene of South and Southeast Asia. Pickford (1988) has united the Siwalik material of *Propotamochoerus* into a single species, *P. hysudricus*. In this definition, *P. hysudricus* would be a species with an important size variation (see measurements in Pickford, 1988) with a long temporal and geographical range. Alternatively, other authors (e.g., Made et al., 1999; Sein et al., 2009) consider that *P. hysudricus* could represent more than one species. Since the work of revision of *P. hysudricus* is out of the scope of our work, we used the taxon name *P. hysudricus* for the Haritalyangar material.

***Hippopotamodon* Lydekker, 1877**

***Hippopotamodon sivalense* Lydekker, 1877**

Holotype GSI B7 left maxilla fragment with P4–M2.

Distribution and temporal range Late Miocene of South Asia (India, Pakistan) and Southeast Asia (Myanmar, Thailand; Chaimanee et al., 2004; Jaeger et al., 2011; Chavasseau et al., 2013); 10.2–7.1 Ma in the Potwar plateau (Siwaliks of Pakistan) (Barry et al., 2002).

New materials HTA-20, right upper molar fragment (M3?); HTA-63, right dp4 on a mandibular corpus fragment.

Description of the new material The molar fragment is very large and is probably a M3 judging by its narrower second lobe. This tooth and possesses massive cusps that present moderately deep furrows. The mesial cingulum is thick. It does not reach the lingual side of the tooth. A broken accessory cusp is present between the protocone and the metaconule at the end of the transverse valley and contributes to a lingual bulge of the tooth.

The dp4 HTA-63 (Fig. 2I, J) has large dimensions (length: 31.1 mm; breadth: 15.5 mm) and is trilobate. The cusps are massive. The mesial lobe is constituted of three cusps: large and equal-sized primonid and paraconid, and a smaller and centrally positioned preprimonid. An endoparaconulid is present in the valley between the two mesial lobes. This cusp is not much inflated and does not block the transverse valley. There is no transverse connection between the hypoconid and entoconid due to a weak endoentocristid and the absence of an endohypocristid. In the talonid, a large mesoconulid is present. This cusp is laterally expanded and connected by a weak crest to a buccal accessory cusp. The hypoconulid is large and distally protruding cusp connect to the hypoconid by a posthypocristid. A buccal cingulid is present between the paraconid and the protoconid and between the protoconid and the hypoconid.

Discussion Few very large-sized suids are known in the Middle Siwaliks. The giant tetraconodontine *Tetraconodon* can be excluded because it does not possess large cusps at the ends of the transverse valleys. This suid has also shallow molar furrows contrary to the

Haritalyangar specimen. The dp4 displays very similar size and morphological characteristics (blunt cusps, well-expressed preprimonid, distinct endoparaconulid, large and transversely expanded mesoconulid, absence of connection between hypoconid and entoconid, large and protruding hypoconulid, presence of a partial buccal cingulid) than those of *Hippopotamodon sivalense* (e.g., H-GSP 330), a giant suine present in the Late Miocene of the Siwaliks. Thus, the Haritalyangar material is identified as belonging to this species.

Family Incertae sedis

***Yunnanochoerus* Made and Han, 1994**

***Yunnanochoerus dangari* Prasad, 1970**

Holotype Lower jaw fragment GSI 18078.

Type-locality and horizon Haritalyangar, Middle Siwalik, Late Miocene (ca. 9 Ma).

Emended diagnosis (after Pickford, 2011) Medium-sized suoid with bilophodont lower molars. Lophodonty not fully achieved (longitudinal valleys across lophids still visible, base of the cusps still rounded). Short and mesial preprotocristid on m2. Absent paraconid and mesoconulid on m2/m3. Mesiostylid present mesially to the metaconid m2/m3. Sharp cristid obliqua terminating between the protoconid and the metaconid and connecting the mesial lophid on m2/m3. m2 about as long as m3. Hypoconulid on m2 as a large and distally protruding cusp. Third lobe on m3, short, low with a large and central hypoconulid. Buccal cingulid variably developed on lower molars (absent to subcomplete but weak cingulum). Smooth molar enamel. Differs from the other species of *Yunnanochoerus* by a larger size, a proportionally shorter m3 relative to m2, a large, a distally protruding hypoconulid on m2, and the presence of a buccal cingulid on lower molars. Further differs from *Y. yuanmouensis* by a molar lophodont molar pattern and from *Y. gandakasensis* by a shorter and third lobe on m3. Differs from the suoid *Schizochoerus* by a lesser accentuated lophodonty and more cuspidate hypoconulids on m2/m3. Differs from *Taucanamo* by its lophodont pattern, the absence of a mesoconulid on lower molars. Differs from lophodont suids by extreme reduction of the paraconid, the lack of a mesoconulid, and a low hypoconulid.

New material HTA-154, left lower jaw fragment with m2–m3 (Fig. 3).

Description The molars are low-crowned but possess a pronounced relief due to their acute cusps and lophodonty. The m2 presents a bilophodont occlusal pattern. However, the median valley between the protoconid and the metaconid is still distinct. The valley between the hypoconid and the entoconid is shallower but not completely obliterated by lophodonty. Mesially, a weak cingulid is present with a tiny mesiostylid located against the metaconid. The preprotocristid is short and mostly mesiodistal. No paraconid is visible. The cristid obliqua is sharp and extends up to the trigonid wall where it connects to the mesial lophid between the protoconid and the metaconid. A low but distally protruding hypoconulid is present. This cusp overlaps with the mesial part of the m3 crown. There is a weak but subcomplete buccal cingulid. The m3 has broken protoconid and metaconid. The occlusal pattern of this tooth is most similar to that of m2 except for a lower and narrower second lobe relative to the trigonid.

The third lobe is short, low and presents a larger and more inflated hypoconulid than on the m2. Two lateral crests and a mesial prehypocristulid depart from this cusp.

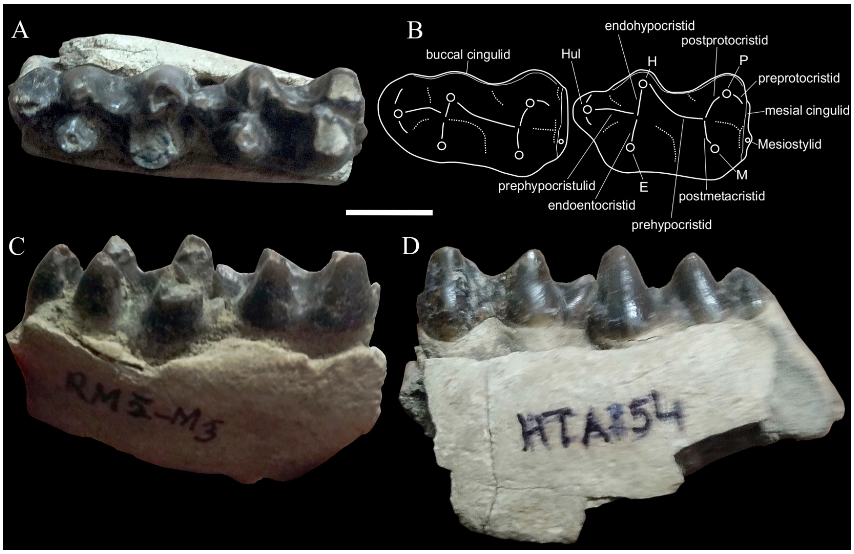

Fig. 3 New material of *Yunnanochoerus dangari* from Haritalyangar
A–D. HTA-154, left mandible with m2–m3: A. occlusal view; B. interpretive drawing; C. lingual view; D. buccal view. Scale bar equals 1 cm. See Fig. 2 for abbreviations

Discussion The new material corresponds to a suoid with lophodont and narrow molars possessing a high molar relief. An identical morphology is found in *Yunnanochoerus*, a poorly-known genus present in Southern China and in Southern Asia during the Late Miocene (Made and Han, 1994). The new Haritalyangar material differs from other fossils referred to *Yunnanochoerus* by a larger size (*Y. gandakasensis* Pickford, 1976, *Y. lufengensis* (Han, 1983), *Y.* sp. from Yuanmou (Pan et al., 2006)), a more pronounced lophodonty (*Y.* sp. from Yuanmou), large m2 and m3 hypoconulid (*Y. lufengensis*, *Y.* sp. from Yuanmou) and short a m3 third lobe (*Y. gandakasensis*). In contrast, the new material matches the rare suoid from Haritalyangar, *Y. dangari*. This taxon was orginally described as an anthracothere by Prasad (1970) and was later transferred to *Yunnanochoerus* by Pickford (2011) who referred additional specimens to this species from the same area retrieved in the GSI collections in Calcutta. The new material corresponds perfectly in size and morphology to GSI HTu and GSI K15/247+249 Pickford (2011:figs. 17, 18; table 4) and provides the first complete m3 known for this species. *Yunnanochoerus dangari* also possibly occurs in the Potwar plateau of the Pakistan Siwalik, a few specimens (H-GSP 14499, H-GSP 4630) do not matching the morphology of the locally best-known species of *Yunnanochoerus*, *Y. gandakasensis*, and better corresponding to *Y. dangari*. These specimens from the Siwaliks of Pakistan are also larger than the holotype of *Y. gandakasensis* and better match in size the material from Haritalyangar. The status of *Y. dangari* is still under debate, this species being not recognized in some recent suoid

classifications (e.g., Made, 2020). However, we adopt here the classification of Pickford (2011) because we consider that the combination of morphology and size displayed by the *Yunnanochoerus* material from Haritalyangar is distinctive.

The familial affinities of *Yunnanochoerus* are also problematic: some authors classified this genus within the family Palaeochoeridae (e.g., Made, 1997; Pickford, 2011) while Liu (2003) proposed to include it in the Suidae. The phylogenetic analysis of Orliac et al. (2010) retrieved the Palaeochoeridae (*Schizochoerus* excluded) as a monophyletic or paraphyletic group out of the Suidae. Because the validity of the Palaoechoeridae is not fully demonstrated and its composition still under debate, we preferred leaving *Yunnanochoerus* with an uncertain familial ranking in this work.

4 Discussion and conclusions

Three suoid taxa, *Propotamochoerus hysudricus*, *Hippopotamodon sivalense* and *Yunnanochoerus dangari*, can be identified in the new material from the area of Haritalyangar. Although the presence of these taxa had been previously recognized in this area, this was based on very few specimens. For instance, Pickford (1988) reported two specimens from Haritalyangar to *Propotamochoerus hysudricus* and five specimens to *Hippopotamodon sivalense*. Thus, the new material brings valuable new information on the Haritalyangar suoids. The new material of *P. hysudricus* represents the most complete locally known specimens of this species. They indicate that *P. hysudricus* from Haritalyangar has a wide spectrum of size ranges (e.g., 35% of variation on m1 length), similarly to the metric range observed in the Siwaliks of Pakistan (e.g., 30% of variation on m1 length). The m1 dimensions of *P. hysudricus* from Haritalyangar allow estimating a bodymass range for this species of 92–194 kg (mean=133 kg; N=4 including the measurements for GSI 18082 from Pickford, 1988). Other equations based on m2 length and M2 length allow estimating a range bodymass for Haritalyangar material of 97–203 kg (mean=158 kg, N=3) and 118–123 kg (mean=120 kg, N=3), respectively (see also Table 3).

The suoid *Yunnanochoerus dangari* is a very rare taxon, previously known in Haritalyangar by three specimens. The new lower fragment reveals additional morphological characteristics of this species by documenting the first complete m3 for this species. Body masses of 61 kg for holotype GSI 18078 and 74 kg for GSI K15/247+249 can be estimated based on m1 area. The bodymasses estimated with the length of m2 are higher (mean=114 kg, N=3; Table 3). The relatively small body mass and the brachyodont and lophodont molars of *Yunnanochoerus dangari* suggest that it was a specialized folivorous suoid, thus exploiting a different ecological niche than the larger and omnivorous suids *P. hysudricus* and *H. sivalense* (Nelson, 2003).

In addition to the taxa identified herein, the tetraconodontine suids *Tetraconodon magnus* and *Lophochoerus nagrii* are also known from Haritalyangar. This suoid faunal association is typical of the Middle Siwaliks and best corresponds that found in the Nagri Fm. of the

Potwar. In this formation, the suoid fauna comprises *Propotamochoerus hysudricus* and *Hippopotamodon sivalense* as the two most common species together with *Tetraconodon magnus*, *Yunnanochoerus gandakasensis*, and possibly *Y. dangari*. In addition, Pickford (2011) attributed a maxilla from Nagri to the species *Lophochoerus nagrii.* Hence, all of the suoids from Haritalyangar can be found associated in the Nagri Fm. First occurrence-Last occurrence brackets of *Yunnanochoerus*, *Hippopotamodon sivalense*, *Propotamochoerus hysudricus* and *Tetraconodon magnus* are respectively 10.1–8.7 Ma, 10.2–7.2 Ma, 10.2–6.8 Ma and 10.0–9.3 Ma in the Potwar plateau (Barry et al., 2002). Our new data indicate that the suids *Propotamochoerus hysudricus* and *Hippopotamodon sivalense* are recorded record from both the 'Lower Alternations' and 'Upper Alternations'. On the contrary, *Yunnanochoerus dangari* is only known from the 'Lower Alternations' beds near the city of Dangar. According to Pilgrim (1926), the *Lophochoerus* specimen originates from the "Nagri zone of Haritalyangar" which probably corresponds to the 'Lower Alternations'. Thus, considering these biochronological and biostratigraphical data, an age bracket of 10–8.7 Ma (temporally corresponding to the upper half of the Nagri Fm. and the base of the Dhok Pathan Fm.) can be given to the 'Lower Alternations' of Haritalyangar based on suoids. The two suid species recovered from the 'Upper Alternations' are long-living taxa throughout the Late Miocene. Their co-occurrence reasonably indicates a maximum age of 7 Ma for the top of the Haritalyangar section. The age brackets provided by suoids are close to the correlation to the GPTS of the magnetic polarity data preferred by Brozovic and Brubank (2000) and Pillans et al. (2005). These authors dated the most of the section of Haritalyangar between about 10 and 8 Ma and the hominoid-bearing interval, from which some of the suoid material originates, between 9.2 and 8.6 Ma. An alternate correlation to the GPTS was proposed by Johnson et al. (1983), which implied a slower sedimentation rate, dated the Haritalyangar section between 10 to 6 Ma. This correlation, which was involving diachronous ranges for *Sivapithecus* between the Siwaliks of India and Pakistan (Pillans et al., 2005), does not match well our data by also implying

Table 3 Estimated body masses for the Haritalyangar suoids based on regressions of Legendre (1989) and Damuth (1990) (kg)

Specimen	Taxon	Body mass (m1 area)	Body mass (m2 length)	Body mass (M2 length)	Body mass (M1 area)
HTA-8	*P. hysudricus*	94.5	96.6		
HTA-126b	*P. hysudricus*	194.4	202.9		
HTA-141	*P. hysudricus*	135.6	175.7		
GSI 18082	*P. hysudricus*	114			
HTA-140a	*P. hysudricus*			119.8	
HTA-140b	*P. hysudricus*			118.2	
HTA-42b	*P. hysudricus*			123.3	
HTA-126a	*P. hysudricus*				67.9
GSI 18078	*Y. dangari*	60.5			
GSI K15/247+249	*Y. dangari*	73.7	108.9		
GSI Htu	*Y. dangari*		107.2		
HTA-154	*Y. dangari*		126.9		

See section material and methods for equations. Body masses calculated for GSI specimens based on measurements from Pickford (2011).

diachronous last occurrence of all suoids compared with the Potwar plateau. Recently, Sankhyan and Chavasseau (2018) identified a putative *Stegodon* upper molar fragment from the top of the 'Upper Alternations' and indicated that it could suggest a younger age for this part of the section than in the preferred correlation of Brozovic and Brubank (2000) and Pillans et al. (2005). However, the identification of *Stegodon* is uncertain and does not represent enough evidence to challenge this correlation (that is consistent with our suoid data). An alternative possibility is that the boundary between the 'Upper Alternations' and the Boulder Conglomerate is diachronous and is significantly younger than 8 Ma in the area of Dholkhana, Bhapral, and Barog where the proboscidean fossil was discovered. Only further fossil material with precise stratigraphic provenience will allow testing this hypothesis.

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印度Haritalyangar地区晚中新世猪类化石新材料

Anek R. SANKHYAN[1] Olivier CHAVASSEAU[2]

(1 古生物研究会 古马尔温 174021, 喜马偕尔邦, 印度)

(2 法国普瓦蒂埃大学，法国国家科研中心UMR 7262 普瓦蒂埃市 86073, 法国)

摘要：描述了印度北部比拉斯布尔区喜马偕尔邦Haritalyangar地区中西瓦利克的猪类化石上、下颌及牙齿材料。Haritalyangar地区以晚中新世动物群、古人类和其他灵长类动物的多样性而闻名。研究材料为作者之一(ARS)在该地区多次野外季采集的猪类化石；猪类化石地点和最近报道的长鼻类化石地点(含古猿化石地点)也被绘制在地图上。这些化石地点广泛分布于Makkan Khad到 Sir Khad区域内的"Lower Alternations"层和"Upper Alternations"层。猪类化石被鉴定为三个属：*Propotamochoerus* (*P. hysudricus*)、*Hippopotamodon* (*H. sivalense*) 和*Yunnanochoerus* (*Y. dangari*)。 *Propotamochoerus hysudricus* 为中西瓦利克最常见的化石猪类，新发现的*Yunnanochoerus dangari*化石进一步证明这种古猪类化石仅在Haritalyangar地区有少量遗存。Haritalyangar地区新发现的猪类化石组成与巴基斯坦的Nagri动物群相近。基于猪类化石进行的的Potwar高原年代地层学对比表明，Haritalyangar地区的"Lower Alternations"层的年龄范围为~10–9 Ma, 与最新的磁极性地层学年代范围很接近。

关键词：中西瓦利克，晚中新世， 猪超科，云南猪属，原河猪属，河马齿河猪属

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